

MORPHOLOGICAL ANALYSIS AND PHYTOGEOGRAPHY OF NATIVE
CALAMAGROSTIS (POACEAE) FROM BRITISH COLUMBIA, CANADA AND
ADJACENT REGIONS

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ABSTRACT

The taxonomically difficult and ecologically and phytogeographically important genus, *Calamagrostis*, was examined for British Columbia (BC). Morphological characters were analyzed by Principal Components Analysis (PCA) to characterize taxa and to aid in the development of a new key. Eight native species (*Calamagrostis canadensis*, *C. lapponica*, *C. montanensis*, *C. nutkaensis*, *C. purpurascens*, *C. rubescens*, *C. sesquiflora*, and *C. stricta*) are confirmed to occur in British Columbia, of which *C. montanensis*, *C. nutkaensis*, *C. purpurascens*, *C. rubescens*, and *C. sesquiflora* are reliably distinguishable. Comparison of species distribution to regional climatic and vegetation history suggests that *Calamagrostis nutkaensis* and *C. sesquiflora* likely survived in coastal refugia during late Wisconsin glaciations. *Calamagrostis purpurascens* likely persisted beyond the glacial limits or within nunataks and then spread into previously glaciated sites. Two interior continental species, *C. montanensis* and *C. rubescens*, probably spread north and west from the unglaciated zone south of the Cordilleran and Laurentide ice sheets. *Calamagrostis lapponica* likely persisted north of the ice sheets, and then spread southward into high-elevation sites in northern and eastern BC. *Calamagrostis canadensis* and *C. stricta* probably survived south and north of the ice sheets, and then spread into the previously glaciated terrain.

Key Words: British Columbia, *Calamagrostis*, phytogeography, Poaceae, principal components analysis.

Calamagrostis Adans. (reed grass) is a widespread northern hemisphere genus of approximately 100 species (Marr et al. 2007) mainly of the temperate and Arctic zones (Hitchcock et al. 1969; Scoggan 1978; Tsvelev 1984; Greene 2001). Twenty-five native and one introduced species occur in North America north of Mexico (Marr et al. 2007). As circumscribed by Greene (2001), eight native species occur in British Columbia: *Calamagrostis canadensis* (Michx.) P. Beauv., *C. lapponica* (Wahlenb.) Hartm. *C. montanensis* (Scribn.) Scribn., *C. nutkaensis* (J. Presl) J. Presl ex Steud., *C. purpurascens* R. Br., *C. rubescens* Buckley, *C. sesquiflora* (Trin.) Tzvelev, and *C. stricta* (Timm.) Koeler. Two intraspecific taxa are recognized within *C. canadensis* and *C. stricta*. Species are primarily distinguished according to spikelet length, the length of the awn relative to the lemma, the position of attachment of the awn, whether the awn is bent or straight, and callus

hair length relative to lemma length (Hultén 1968; Hitchcock et al. 1969; Clarke 1980; Tselev 1984; Marr et al. 2007). In 2005, *Calamagrostis epigeios* (L.) Roth, a Eurasian species, was collected for the first time from BC (British Columbia, Lower Mainland, Chilliwack, Fraser River, unnamed island in Fraser River N of Chilliwack, 49°12'18"N, 121°57'33"W, 28 Aug 2005, Frank Lomer s.n. (V195593)). It and the recently introduced horticultural plant *C. x acutiflora* (Schrad.) DC., of Eurasian origin, are not included in this study (but see Marr et al. (2007)).

Calamagrostis species in BC occur in diverse habitats including alpine tundra, coastal bluffs, wetlands, coniferous forest, steppe and meadows. Several species have prominent ecological roles because of their abundance, their characteristic associations with key regional ecosystems (Meidinger and Pojar 1991), and their ability to colonize following disturbance (Tsvelev 1984; MacDonald and Lieffers 1991). In the United States, natural stands of *C. rubescens*, *C.*

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montanensis, and *C. inexpansa* A. Gray (= *C. stricta*) provide forage, and *C. canadensis* is a source of wild hay (Hitchcock 1971). Specimen labels from DAO (Agriculture and Agri-Food Canada Herbarium, Ottawa, Ontario) indicate that in the 1970's Agriculture Canada evaluated accessions of *C. canadensis*, *C. purpurascens*, and *C. stricta* from western Canada, in common garden plots in Beaverlodge, Alberta, presumably to bring these species into cultivation as forage. *Calamagrostis sesquiflora* is of notable phytogeographical interest because its restricted distribution may provide clues to the region's glacial history and subsequent colonization by plants (Ogilvie 1997).

For these reasons, the identification of *Calamagrostis* species is particularly important, however many have observed that species determinations are difficult. For example, Stebbins (1930:35) observed that *Calamagrostis* species "are exceedingly variable and difficult to define", while Hitchcock et al. (1969:522) noted that "several species are highly variable and mutually distinguishable only with some difficulty". In western Canada, the species of the "*C. canadensis*/*C. stricta*/*C. lapponica* complex" are especially challenging to distinguish. Within *C. canadensis* and *C. stricta* it is also difficult to assign many specimens to a subspecific rank *sensu* Greene (2001). In the Royal British Columbia Museum herbarium (V) many specimens were identified to the wrong species or subspecies, suggesting that published keys may not be adequate to separate taxa reliably. For example, many character states by which the subspecific taxa of *C. canadensis* and *C. stricta* are differentiated overlap greatly (Greene 2001).

Classification of some North American species is difficult, in part, due to apomixis, hybridization and polyploidy (Nygren 1954; Clarke 1980; Greene 1984; Tsevlev 1984) which likely generate and perpetuate numerous closely related genotypes that differ from each other by relatively subtle differences. A description of the genus can be found in Marr et al. (2007). Multiple chromosome counts have been reported for the species that occur in BC (Nygren 1954; Kawano 1965; Moss 1983; Greene 1984): *C. canadensis* ($2n = 42, 45, 48, 49, 51, 56, 62, 65$); *C. lapponica* ($2n = 28, 42, 49-140$); *C. montanensis* ($2n = 28$); *C. nutkaensis* ($2n = 28$); *C. purpurascens* ($2n = 40-42, 47-49, 50, 53, 56, 54, 84$); *C. rubescens* ($2n = 28, 42, 56$); *C. sesquiflora* ($2n = 28$); *C. stricta* ($2n = 28, 56, 70, 84, \text{ca. } 104, \text{ca. } 114, \text{ca. } 120, \text{ca. } 123$). Polyploidy and especially aneuploidy occur in those taxa that are difficult to distinguish, namely *C. canadensis*, *C. lapponica* and *C. stricta*.

We undertook a systematic examination of British Columbia *Calamagrostis* species, based largely on a multivariate analysis of morphological characters. Our goals were to develop a better

key and species descriptions, to evaluate intra-specific taxa in *C. canadensis* and *C. stricta*, and to more accurately map species distributions. We examine the phytogeography of the genus in northwestern North America and discuss it in the context of current understandings of the regions glacial, environmental and climatic history (Hebda 1995, 1997; Byun et al. 1997; Whitlock and Bartlein 1997; Heusser et al. 1999; Heinrichs et al. 2002). The results presented here are the basis for the measurements and a portion of the key presented in the Flora of North America treatment for those *Calamagrostis* species that occur in British Columbia (Marr et al. 2007).

METHODS

Morphology

We examined and recorded label data from 1900 specimens from multiple herbaria: V, DAO, CAN, OLYM, SMI, UAC and UBC. We concentrated on specimens from British Columbia, but included selected material from Alaska, Washington, Yukon, Alberta, and Russia (four specimens originally determined as *C. langsdorfii* (Link) Trin. that were annotated by C. W. Greene in 1991 as *C. canadensis* var. *langsdorfii* (Link) Inman). We also observed species habitats and sampled populations during fieldwork in British Columbia from 2002–2009. No type specimens were viewed.

Under magnification, we measured and observed 24 characters (Table 1) from 247 specimens (Appendix 1), initially accepting as correct the most recent name on the sheet. Data were analyzed by Principal Components Analysis (PCA) using SYSTAT (Wilkinson 1997). Individuals were plotted according to their scores from the first two PCA axes. Taxa whose specimens mostly grouped together and were distinct from other taxa in the scatter-plot were removed from the data set. The PCA was repeated a second time using the revised data set. By removing the specimens of the more distinct species we hoped to achieve some resolution among the specimens of the remaining taxa, i.e., those that were less distinct in the scatter-plot. This procedure was repeated a third time. For the second and third PCA an additional character, "glume width" (GW) was added because the ratio of glume length to glume width appeared to be useful to distinguish among the taxa included in these PCA's. The character, "awn exerted versus not exerted" (AWNEXRT), was removed for the second and third PCA's because all specimens of the species included in these PCA's shared the same character state (awns were not exerted).

If a specimen's position on the scatter-plot differed from others of the same taxon, or if it

TABLE 1. CHARACTERS MEASURED ON SPECIMENS OF BC *CALAMAGROSTIS* TAXA FOR PRINCIPAL COMPONENTS ANALYSIS (MARKED BY "+") AND TAXONOMIC DESCRIPTIONS. Characters marked by "*" are those used by Greene (2001).

Character	Character code	Character description
Inflorescence	+*INFL	length
	+INFW	width
	+RACH	rachis surface: 1 = sparsely scabrous; 2 = very scabrous, with longer, twisted projections
	+*BRL	longest branch from the most basal inflorescence node
First glume	+*GL	length
	+GW	width
	GLWRAT	length/width ratio
	GVERSUSL	glume length minus lemma length
	+GSR	glume surface: 1 = glabrous; 2 = scabrous keels only; 3 = whole surface scabrous; 4 = scabrous projections longer and bent
Lemma	+LML	length
	+HARL	callus hair length
	*HRAT	callus hair length/lemma length
	+AWNATT	distance from base of lemma to point of attachment of awn
	AWBSRAT	distance from base of lemma to point of attachment of awn/lemma length
	+*AWNVRT	extent of awn exertion beyond glume margin: 1 = not exerted; 2 = exerted
	+*DIR	awn: 1 = straight; 2 = bent
Flower	+AWNL	awn length
	ALRAT	awn length/lemma length
	+ANTHL	anther length
Leaf	+LFW	width of second leaf below inflorescence
	+LFL	length of second leaf below inflorescence
	LL	length of longest leaf on specimen
	WL	width of longest leaf on specimen
	+*BLADE	leaf blade: 1 = involute; 2 = flat
	+LIGT	ligule type: 1 = delicate and lacerate; 2 = stiff and not lacerate
	+*ULFS	upper leaf surface: 1 = glabrous; 2 = slightly scabrous; 3 = very scabrous; 4 = scabrous + slightly pilose; 5 = tomentose
	+*LLFS	lower leaf surface: 1 = glabrous; 2 = scabrous
	+*COLLAR	collar: 1 = glabrous; 2 = scabrous; 3 = pilose; 4 = tomentose
	+LIGULE	ligule surface: 1 = glabrous; 2 = short hairy; 3 = long hairy
	+LIGL	ligule length
Stem	TOTAL HT	total plant height
	+*HT	height from root crown to base of inflorescence
	+CULM	culm surface: 1 = glabrous; 2 = slightly scabrous; 3 = very scabrous
	+*NODE	number of nodes (from the root crown to the inflorescence)

had been collected outside of the main geographical or ecological range of that taxon, it was examined more closely and often, but not always, re-determined as the taxon with which it clustered most closely. Using box plots of each character for each taxon, we noted those characters that overlapped relatively little among taxa and tested the possibility of using these characters as a means of distinguishing among taxa. We repeated these steps through several iterations to minimize the degree of overlap among clusters of the same taxon. This approach assisted us in the preparation of a key. The key was successfully verified in the field during 2002–2008. Once we had established the key, we examined all other specimens that had not been included in the multivariate analysis and made re-determinations as necessary.

Mapping

Latitude and longitude data from confirmed herbarium specimens were entered into a database. Where only place names were given, latitude and longitude were derived from maps, printed gazetteers (Canadian Permanent Committee on Geographical Names 1985) and the web sites <http://geonames.nrcan.gc.ca/> and <http://geonames.usgs.gov/>. After all specimens had been examined and annotated the database was updated with re-determinations. Records were then mapped using ArcView 9a (Environmental Systems Research Institute, Inc. 1992–1999). The map projections used are an Albers Equal Area Conic (Sphere) with a central median of –115 degrees and reference latitude of 51 degrees.

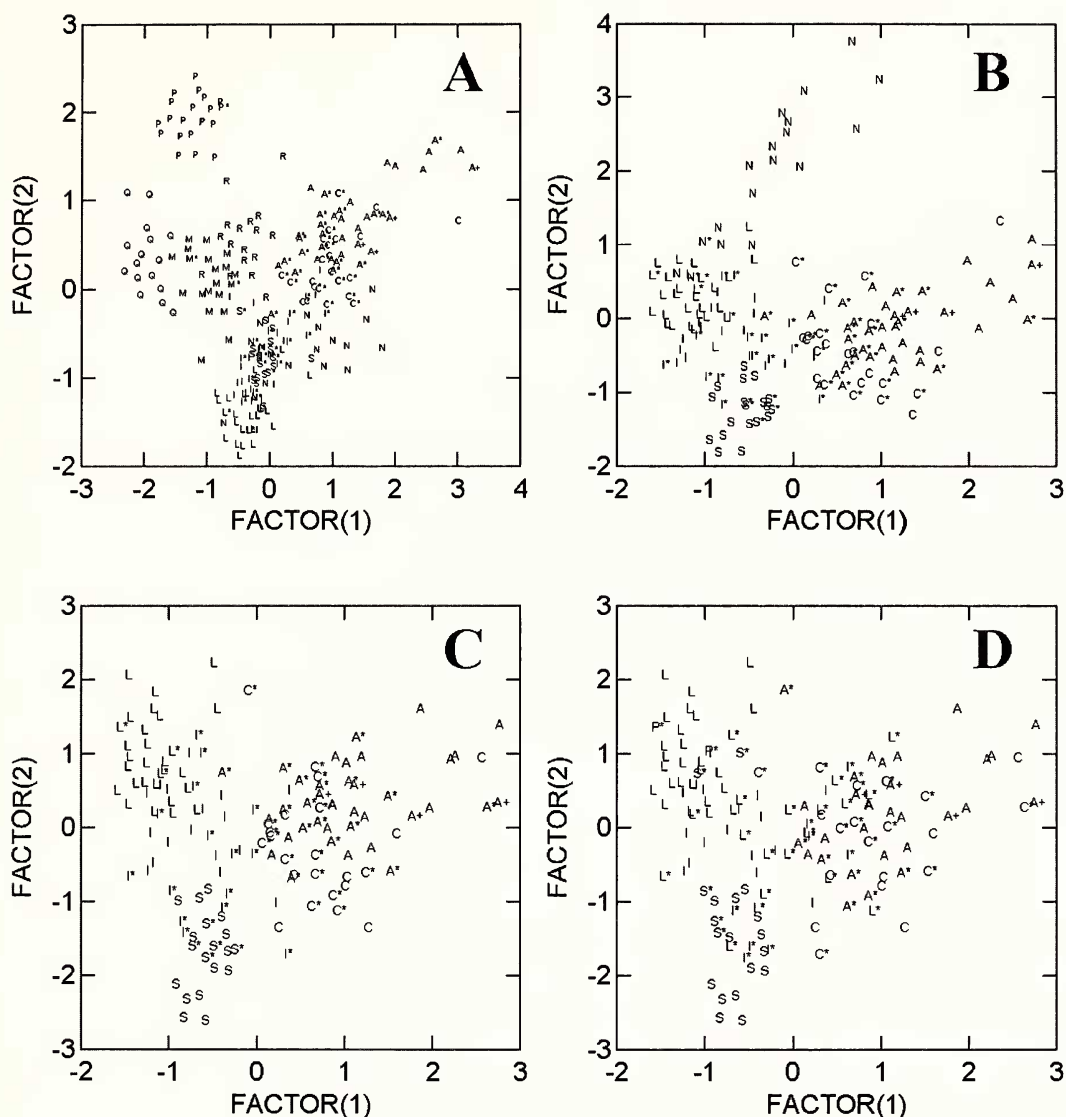


FIG. 1. Principal Components Analysis of morphological characters of native British Columbia *Calamagrostis* species. Letters represents a single specimen: C = *C. canadensis* var. *canadensis*; A = *C. canadensis* var. *langsдорfi*; L = *C. lapponica*, M = *C. montanensis*, N = *C. nutkaensis*, P = *C. purpurascens*, R = *C. rubescens*, Q = *C. sesquiflora*, I = *C. stricta* subsp. *inexpansa*, S = *C. stricta* subsp. *stricta*. The “*” indicates specimens that we have re-determined. Specimens labeled with “+” are from Russia. **A.** All species. **B.** Original data set but with *C. montanensis*, *C. purpurascens*; *C. sesquiflora*, and *C. rubescens* removed. **C.** *C. canadensis*, *C. lapponica*, *C. stricta* only. **D:** Same as Fig. 1C, but with specimens labeled according to the most recent name that was written on the label i.e., prior to this study.

RESULTS

Morphology

In the first PCA (all species), specimens of *C. montanensis*, *C. purpurascens*, *C. rubescens* and to a lesser extent *C. sesquiflora* formed largely discrete clusters (Fig. 1A). *Calamagrostis canadensis* and *C. nutkaensis* also clustered separately to some extent. There was considerable overlap

among *C. stricta*, *C. lapponica* and *C. nutkaensis*. The first axis accounted for 24.8% of the variation with inflorescence branch length (BRL), plant height (HT), and the number of nodes (NODE) contributing the most. The second axis accounted for 19.2% of the variation with ligule type (LIGT), rachis surface roughness (RACH), and glume surface (GSR) contributing the most. The third axis (not shown) accounted for 14.5% of the variation with glume length (GL), leaf

TABLE 2. RANGE OF VARIATION IN MORPHOLOGICAL FEATURES OF *CALAMAGROSTIS* TAXA FROM BRITISH COLUMBIA. Unless otherwise noted, these characters were used in the Principal Components Analysis. See Table 1 for description of character codes. * = PCA2, PCA3 only; ~ = not included in PCA; # = PCA1 only

Character	<i>Calamagrostis</i> taxon (n)				
	<i>canadensis</i> var. <i>canadensis</i> (28)	<i>canadensis</i> var. <i>langsdorfii</i> (34)	<i>lapponica</i> (28)	<i>montanensis</i> (20)	<i>nutkaensis</i> (20)
Inflorescence					
INFL (cm)	(9)11–4(19)	(8)9–15(24)	(4)8–1(16)	(4)7–9(10)	(8)13–3(31)
INFW (cm)	(1)2–3(7)	(1.5)2.5–(8)	(0.7)1–2(2.8)	(0.7)1–2(2.5)	(1.1)2–4.5(9)
BRL (mm)	29–45(57)	(27)35–60(120)	(21)25–35(54)	13–30	27–70(105)
RACH	(1)1.5(2)	(1)1.5(2)	1(1.5)	(1)1.5(2)	1(2)
First glume					
GL (mm)	2.5–.5(4.0)	(3.5)4.0–4.5(5.2)	(3.6)4.0–5.0(5.4)	(3.1)3.5–4.5(5.7)	4.4–6.0(6.6)
~GW (mm)	(0.7)1.0–1.3(1.4)	(0.7)1.0–1.3(1.6)	(1.0)1.3–1.4(1.7)	na	(1.0)1.1–1.3(1.7)
*GLWRAT	(2.1)2.6–3.2(4.0)	(2.7)3.5–4.0(6.7)	(2.6)3.0–3.5(4.4)	na	(3.4)4.0–5.0(5.5)
~GVERSUSL	(0.0)0.3–0.6(1.6)	(0.4)1.0–1.4(2.1)	0.3–1.5(2.3(1.9))	(0.3)0.8–1.2(2.1)	(0.4)0.8–1.3(2.5)
GSR	1–3(4)	(1)2–4	(0)1–(2)	1–3(4)	1(2)
Lemma					
LML (mm)	(2.2)2.7–3.1(4.0)	(2.3)2.5–3.0(4.0)	(2.5)3.0–3.8(4.7)	(2.7)2.9–3.5(3.8)	(3.0)4.0–4.5(4.8)
~HARL (mm)	(1.7)2.5–2.9(3.1)	(1.5)3.0–3.3(4.5)	(2)3.0–3.5(4.7)	(1.2)1.7–2.1(2.4)	(1.1)2.0–2.5(2.9)
~HRAT	(0.7)0.9–1.1(1.4)	(0.5)1.0–1.2(1.5)	(0.6)0.8–1.0(1.2)	0.4–0.8(1.3)	(0.2)0.5–0.7(1.0)
AWNATT (mm)	0.3–1.0(1.6)	(0.3)0.5–1.3(1.7)	(0.3)0.8–1.2(1.6)	0.5–1.0(1.8)	(0.7)1.1–1.9(3.1)
~AWBSRAT	(0.1)0.2–0.4(0.7)	(0.1)0.2–0.4(0.5)	(0.1)0.2–0.4(0.6)	(0.1)0.2–0.3	(0.1)0.3–0.4(0.5)
#AWNVRT	no	no	no	sometimes	no
DIR	1	1	1(2)	2	1
AWNL (mm)	1.9–2.6	(1.7)2–3.1	1.4–3.1	(1.0)2.0–3.1	1.0–3.2
~ALRAT	(0.6)0.9–1.1(1.4)	(0.8)1.0–1.1(1.4)	(0.6)0.8–1.1	(0.7)1.0–(1.2)	(0.6)0.7–0.9(1.3)
Flower					
ANTHL (mm)	(0.8)1.2–1.3(2.0)	(0.9)1.2–1.6(2.6)	(1.1)1.3–1.7(2.0)	(1.1)1.8–2.4(2.5)	(1.0)2.4–2.6(3.3)
Leaf					
LFW(mm)	(2)3–5(8)	(2)3–6(10)	(1.5)2.0–3.5(4.0)	(1)2–(3)	(2)4–10(13)
~WL(mm)	2.5–5(6)	(2)4–7(11)	2.5–3.5	2–3	(3)4–10(20)
LFL(cm)	(11)16–24(41)	(11)18–24(48)	(4)8–12(21)	(5)8–11(18)	(4)18–40(52)
~LL(mm)	(9)22–31(40)	(14)21–29(50)	(10)13–17(26)	(10)12–19(23)	(15)31–41(56)
BLADE	flat	flat	flat	usually folded	flat
LIGT	lacerate	lacerate	usually entire	entire	usually entire
LIGL(mm)	(1)4–6(12)	(3)5–8(12)	(0.5)2–3(6)	(1)2–4(5.5)	(0.5)2–3(5.5)
LIGULE	1–3	(1)–3	1–(2)	(1)2–3	1–3
ULFS	(1)3–4	(1)3–4	(1)2(4)	(1)2–3	1–2
LLFS	2	2	1	2	1
Stem					
HT (cm)	(36)55–70(145)	(18)50–90(154)	(8)20–40(69)	(9)20–25(44)	(31)45–85(111)
~TOTAL HT (cm)	(50)65–80(160)	(45)65–110(180)	(23)35–50(80)	16–40(54)	(42)55–105(135)
CULM	1–2(3)	1–2	1	(1)2–3	1–3
NODE	(2)3–4(6)	(2)3–5(7)	1–2(3)	1–2	1–2(3)

width (LFW) and anther length (ANTHL) contributing the most.

In the second PCA, *C. montanensis*, *C. purpurascens*, *C. rubescens* and *C. sesquiflora* were removed from the data set. In this analysis, *C. nutkaensis* and to some extent *C. lapponica* were distinct. *Calamagrostis canadensis* and *C. stricta* were largely distinct at the species level; however, there was more overlap at the intraspecific level (Fig. 1B). The first axis accounted for 27.1% of the variation with number of nodes (NODE), LIGT and GSR contributing the most. The second axis accounted for 19.2% of the

variation with GL, lemma length (LML) and ANTHL contributing the most.

For the third PCA *C. nutkaensis* was removed from the data, leaving *C. canadensis*, *C. stricta*, and *C. lapponica*. *Calamagrostis lapponica* formed a relatively discrete cluster; however there was some overlap with specimens of *C. stricta* and *C. canadensis* (Fig. 1C). There was little overlap between *C. canadensis* and *C. stricta*. Relative to *C. lapponica*, and to a lesser extent to *C. stricta*, *C. canadensis* was the most variable species. The first axis accounted for 33.0% of the variation with NODE, LIGT, and LIGL contributing the most.

TABLE 2. EXTENDED.

<i>Calamagrostis</i> taxon (n)				
<i>purpurascens</i> (21)	<i>sesquiflora</i> (20)	<i>rubescens</i> (18)	<i>stricta</i> subsp. <i>inexpansa</i> (33)	<i>stricta</i> subsp. <i>stricta</i> (17)
(4)7-9(13)	(4)7-9(11)	(5)9-13(24)	(6)8-11(18)	(4)8-0(13)
0.9-2(2.8)	0.8-2.5(2.8)	(0.7)1.5-(2.7)	(0.8)1-2(2.8)	(0.7)1-2(2.5)
13-25(34)	15-30	(12)20-0(100)	16-50	(14)20-25(33)
2	(1)1.5(2)	1-1.5(2)	1-1.5	1-1.5
(4.5)5.5-6.5(7.4)	(5.3)6.0-8.5(9.5)	(3.2)4.0-4.5(5.1)	3.0-4.0(4.8)	(2.2)2.5-3.0
na	na	na	(0.9)1.2-1.5(2.0)	(0.8)1.0-1.1
na	na	na	(1.9)2.5-3.0(3.6)	(2.0)2.4-2.8(3.2)
(0.5)1.1-1.8(4.5)	(0.5)1.3-2.5	(0.5)1.1-1.9	0.1-1.0(1.4)	0.1-1.5(1.6)
(1)2.5-4	1-2	1(2)	1-2(3)	1-2(3)
(3.4)4.1-4.6(5.0)	(3.4)4.8-5.8(6.8)	2.4-3.4	(2.4)2.7-3.5(3.8)	(1.9)2.2-2.5(3.0)
(0.9)1.2-1.5(2.4)	(0.8)1.2-1.8(3.0)	(0.7)1-1.4(2.3)	(1.8)2.3-2.9(4.2)	(1.2)1.5-2(3.0)
0.2-0.4(0.6)	0.1-0.4	0.2-0.5(0.9)	(0.5)0.7-0.9	(0.5)0.7-0.8
(0.3)0.5-1.0(1.4)	(0.5)1.0-1.5(2.5)	(0.3)0.4(1.2)	(0.2)0.5-1.2(2.3)	(0.3)0.7-1.1(1.3)
0.1-0.2(0.3)	(0.1)0.2-0.3(0.7)	0.1-0.2(0.5)	(0.1)0.2-0.4(0.7)	(0.1)0.3-0.5
yes	yes	usually	no	no
2	2	2	1(2)	1(2)
(4.4)6.0-7.0(9.0)	(5.4)7.0-11.0(13.0)	2.1-3.0(4.4)	0.9-2.6	1.4-2.5
(1.0)1.5-1.8(2.2)	(1.3)1.6-2.1(3.5)	(1.0)1.2-1.4(1.7)	(0.1).8-1.1(1.3)	(0.7)1.0-1.2(1.5)
(1.3)1.7-2.5(2.9)	(1.2)2.2-3.0(3.4)	(1.0)1.3-2.0(2.6)	(0.9)1.5-1.8(2.4)	(1.1)1.2-1.4(1.7)
2-3(5)	(2)3-5(6)	(1)2-5(8)	(1.5)2-3(6)	(1.0)2(2.5)
(2)3-5(6)	(2)4-7	(1.5)3-5(8)	2-5(6)	1.5-3
(4)7-12(17)	(3)8-12(18)	(6)9-20(36)	(5)11-18(28)	(9)18-25
(11)22-27(42)	(9)17-25(31)	(12)24-6(42)	(9)15-24(34)	(12)13-23(25)
flat or folded	flat	usually flat	usually flat	flat or folded
usually entire	entire or lacerate	lacerate	usually entire	entire
(3.5)2-4(9)	(0.5)2-5(6)	(2)3-5(6)	(0.5)3-4(6)	(0.5)1-2(4)
3	1-2(3)	1(2)-3	1-3	(1)2-3
5	1-2	1-3	(1)2-4	(1)2-4
2	1	1-2	1-2	1-2
(20)35-55(70)	19-25(39)	(23)60-70(105)	(22)35-65(88)	(27)35-60(94)
(33)40-65(80)	30-40(46)	(50)70-90(126)	(29)45-75(98)	(35)50-70(100)
(1)2-3	1(2)	1(2)	1-2	1-2
(1)2(3)	1-2(3)	(1)2-3(4)	1-3(4)	1-3(4)

The second axis accounted for 15.3% of the variation with GL, hair length (HARL) and LML contributing the most.

In order to visually evaluate the impact of our analysis upon the identification of the "*C. canadensis*/*C. lapponica*/*C. stricta* complex" we replotted the results of the third PCA, but labeled the points according to the most recent (i.e., prior to our analysis) identification on the sheet (Fig. 1D). The changes that are indicated in this figure include 29 redeterminations at the subspecific category and 32 redeterminations at the species level.

Measurements and observations based on our species determinations, using only specimens from North America, are summarized in Table 2. These data derive from specimens for which measure-

ments were taken for the PCA as well as additional specimens that we observed in cases where those specimens that were measured for the PCA failed to capture values at the lower or upper end of the range of a particular character. In terms of overall stature (i.e., plant height, leaf size, and inflorescence size), *C. nutkaensis* and *C. canadensis* are the most robust of the B.C. species, and *C. montanensis* and *C. sesquiflora* are the smallest. *Calamagrostis sesquiflora* and *C. purpurascens* have the largest florets and the longest awns, and *C. stricta* and *C. canadensis* have the smallest florets and awns. Callus hairs are longest in relation to the lemmas in *C. canadensis*, *C. stricta* and *C. lapponica* and are shortest, usually less than half the length of the lemma, in *C. montanensis*, *C. purpurascens*, *C.*

TABLE 3. ECOLOGICAL AND HABITAT CHARACTERISTICS OF *CALAMAGROSTIS* TAXA IN BRITISH COLUMBIA.

Taxon	Habitat	Associated plants	Topographic setting	Soils	Elevation (m)	Disturbance
<i>Calamagrostis canadensis</i> var. <i>canadensis</i>	Open habitats or openings in forests, rarely in forests; ranging from lakeshore, streamside, floodplain to peat lands; also in thickets.	<i>Alnus</i> , <i>Populus</i> spp., <i>Salix</i> spp., <i>Picea mariana</i> , <i>P. glauca</i> , <i>Pinus</i> spp., less frequently <i>Abies</i> .	Mid slope to mainly base of slope and valley bottom; flat terrain including dry to hygric sites.	All substrate textures including peat except bedrock; mostly acid soils.	0-2250	Roadsides, especially burned forests and muskeg.
<i>Calamagrostis canadensis</i> var. <i>langsdorffii</i>	Wetlands, meadows, open forests, lake, river stream shores; infrequent in thickets, woods, forested wetlands; rare on talus and in rock crevices.	<i>Alnus</i> , <i>Cornus stolonifera</i> , <i>Salix</i> spp., <i>Carex</i> , <i>Picea mariana</i> , <i>P. glauca</i> , <i>Populus balsamifera</i> , heaths.	Largely flat terrain, base of slopes; less frequent on slopes; mostly wet, rarely dry sites.	Mainly gravel and sand, but ranges from bedrock to peat.	0-2250	Bulldozed till, eroding surfaces.
<i>Calamagrostis lapponica</i>	Primarily northern and alpine tundra, infrequent in meadows, along streams, lakeshores. Often associated with low shrubs; only full sun.	Heaths, dwarf, creeping <i>Salix</i> , <i>Betula nana</i> , <i>Dryas</i> , <i>Arctostaphylos alpina</i> , lichens, <i>Picea glauca</i> , <i>Abies lasiocarpa</i> .	Ridge tops to base of slope including xeric to (sub)hygric sites; At southern limits in B.C. favors well-drained ridge crests.	Medium to coarse texture, sand and gravel noted.	30-2286	Borrow pit, sloughing bank.
<i>Calamagrostis montanensis</i>	Mainly prairie or grassland, also dry creek bank, sagebrush flat and woodland (see also Moss 1983), mainly full sun.	<i>Artemisia</i> , other Poaceae.	Ridge crest to valley bottom, especially slopes; mostly mesic to xeric sites.	Sand to clay highly favored, no coarse-textured sites reported.	511-1432	Race-track edge.
<i>Calamagrostis nutkaensis</i>	Open to shaded near-coast beaches, marine and freshwater common in wetlands, especially bogs; also in conifer forest openings and forests; associated with cliffs, bluffs.	<i>Picea sitchensis</i> , <i>Pinus contorta</i> , <i>Thuja</i> , <i>Tsuga</i> , <i>Carex</i> spp., other Poaceae, shrubby heathers such as <i>Ledum</i> and <i>Kalmia</i> ; <i>Sphagnum</i> .	Flat terrain and slope base preferred, but occurs on upper and mid slope sites; largely subhydric to mesic sites.	Bedrock through gravel, sand, clay and peat; wide range of soil chemistry from highly saline to highly acidic.	0-790	Archaeological sites.
<i>Calamagrostis purpurascens</i>	Wide ecological amplitude; alpine tundra, scree, talus, grassland, meadows, thickets, parkland, coniferous and deciduous forest; full sun to shade.	<i>Salix</i> spp., <i>Arctostaphylos uva-ursi</i> , <i>Populus tremuloidea</i> , <i>P. balsamifera</i> , <i>Picea</i> spp. and <i>Pinus</i> .	Mainly ridge-tops to slopes, infrequent on valley floors xeric to submesic but not hygric sites.	All textures except peat; favoring medium to coarse substrates; alkaline and limey soils noted.	230-2600	Gravel pits, roadsides, burned over land.
<i>Calamagrostis rubescens</i>	Forest and parkland; infrequent in fields and meadows; full sun to shade.	<i>Populus tremuloidea</i> , <i>Pseudotsuga menziesii</i> and <i>Pinus contorta</i> , Poaceae.	Slopes and flat sites with mesic-xeric moisture regimes.	Limited data, all textures except perhaps clays.	350-2130	Grazed and logged sites.
<i>Calamagrostis sesquiflora</i>	Open rocky cliffs and knolls preferred; open heath and meadow; colonies on talus and at base of cliffs noted; openings in woods.	<i>Tsuga mertensiana</i> krummholz, peat mounds, <i>Carex nutkaensis</i> , <i>Empetrum nigrum</i> , <i>Geum calthifolium</i> , <i>Erigeron peregrinus</i> , <i>Artemisia norvegica</i> , <i>Ligusticum calderi</i> .	Top to base of slope; dry to moist (runnels) sites.	Rock to coarse substrates preferred; mostly acidic.	0-1000	

TABLE 3. CONTINUED.

Taxon	Habitat	Associated plants	Topographic setting	Soils	Elevation (m)	Disturbance
<i>Calamagrostis stricta</i> subsp. <i>inexpansa</i>	Commonly in meadows or grassland associated with rivers and streams; infrequent on grassy slopes; noted to grow at edge of rather than in wetlands; also in low thickets and generally open woods.	<i>Pinus</i> , <i>Betula</i> , <i>Picea</i> , <i>Populus balsamifera</i> , and <i>P. tremuloides</i> .	Largely of damp, not wet bottomlands and flat terrain, occasional on slopes.	Mainly clay to sand, several collections on gravel; notable association with limy and alkaline soils.	0–1800	Drained wetlands and lake bottoms to clear-cuts, burned over forests and gravel pits.
<i>Calamagrostis stricta</i> subsp. <i>stricta</i>	Moist meadows, fens, less frequent in marsh and bog; occasionally with shrubs; full sun.	<i>Carex</i> notably associated, <i>Salix</i> spp.	Flat valley bottom terrain, rarely on slopes; mesic to mostly hygric.	Strictly on fine textured substrates (sand to clay) or peat; notable on alkaline sites.	450–1478	“Burned muskeg” and “disturbed prairie”.

rubescens, *C. sesquiflora* and *C. nutkaensis*. Of the second group, all but *C. nutkaensis* usually have exerted, bent awns.

Specimens of five species appeared to be viviparous, i.e., some florets contained “plantlets” rather than flowers. Those species and specimens are as follows: *C. canadensis* var. *langsдорffii* (Canada, British Columbia, Blue Canyon Creek, 15 Aug 1972, Taylor, Roy L., Beil, Charles E., Marchant, Christopher J., Oliver 6139 (DAO 199629)); Canada, Northwest Territories, Reindeer Station, Inuvik, 31 Jul 1978, Fred Fodor 1336 (UBC 167838); *C. stricta* subsp. *stricta* (Canada, Yukon, Burwash Landing, S. of Burwash Landing, Kluane L., 5 July 1944, Raup, Hugh M., Raup, L. G. 12261 (CAN 276421)); *C. montanensis* (Canada, Alberta, Cardstom, 2 Aug 1950, W.G. Dore 12258 (DAO 105913)); *C. rubescens* (Canada, British Columbia, Elko, Silver Spring Lake, S of third lake in Lakes chain, 21 July 1996, Roemer, Hans L. 96286A (V169178); Canada, Alberta, Waterton town site, ca. 3 miles NNE of, 9 July 1974, Douglas, George W., Douglas, Gloria G. 7954 (V069747)); Canada, British Columbia, Shuswap Lake, 19 July 1996, Martin, M.E. 1337 (V164711); Canada, British Columbia, Lone Butte, on Bridge Lake Road, 7 miles SE of 100 Mile House, 13 July 1956, Calder, J. A., Kukkonen, I., Taylor, R. L. 18800 (DAO 106488); Canada, British Columbia 100 Mile House, 1 mi. N of 100 Mile House, 5 Sept 1954, Calder, J. A.; Savile, D.B.O.; Ferguson, J. M. 15485 (DAO 106489)); and *C. purpurascens* (Canada, Yukon, Carcross, 15 Aug 1960, Calder, J. A.; Kukkonen, I. 28289 (DAO 106364)). The label of V164711 bears the note “current year’s flowering spike pseudoviviparous previous apparently normal.”

Ecology and Distribution

Re-determinations of herbarium specimens, new collections and observations in the field helped refine the understanding of ecology (Table 3) and distribution of *Calamagrostis* species in the study region (Fig. 2). These results demonstrate that two taxa can occur virtually at the same site but in slightly different habitats and that the distributions of several taxa, in particular *C. lapponica* and *C. sesquiflora*, are more sharply constrained than maps heretofore (Douglas et al. 2002b:131–132) have shown. Most taxa favor open habitats such as meadows, grasslands, wetlands, tundra and shorelines in association with woody vegetation. *Calamagrostis rubescens* favors forest or parkland settings. *Calamagrostis nutkaensis* occurs in shaded forest settings, although it is mostly a species of openings.

Considering moisture, there are two broad groups. Taxa of relatively dry sites include *C. montanensis*, *C. purpurascens*, *C. rubescens*, *C. lapponica*, and *C. sesquiflora* (but under a humid

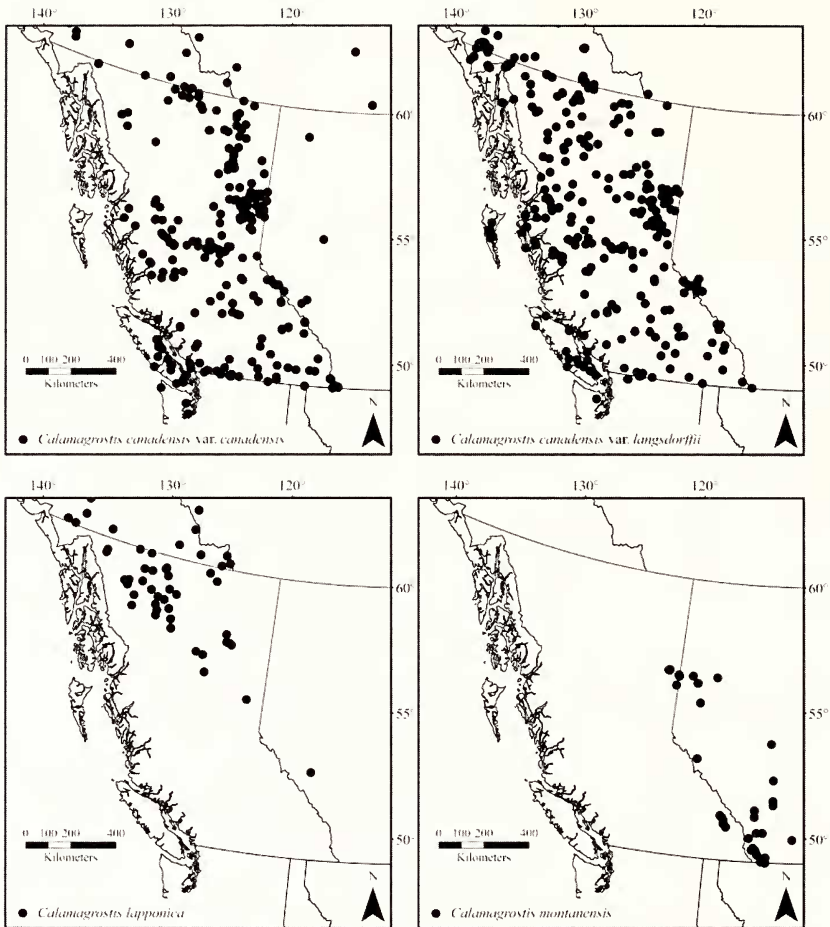


FIG. 2. Distribution maps of species of *Calamagrostis* that occur in British Columbia. Maps do not indicate complete distribution of each species from areas adjacent to, but outside of British Columbia. For complete North American distributions see Marr et al. (2007).

climatic regime). Taxa of relatively moist sites include *C. canadensis* (though not always in the case of var. *canadensis*), *C. stricta* and to a large extent *C. nutkaensis*.

Two species, *C. lapponica* and *C. purpurascens* favor well to moderately drained crest and upper slope positions. *Calamagrostis montanensis* and *C. rubescens* occur mainly on well to moderately drained slopes or flat terrain. *Calamagrostis canadensis* occurs largely on lower slope and mesic to even hydric valley bottom sites. In the alpine of northern BC, we consistently find *C. canadensis* var. *langsдорфii* in moisture receiving sites, local depressions, or beside boulders or tree islands that trap winter snow.

Where *C. lapponica* grows near *C. canadensis*, *C. lapponica* always occurs on a higher slope position and in drier sites. *Calamagrostis montanensis* can grow near *C. canadensis* at the northern limits of its range, but *C. montanensis* occupies warmer, more open and drier sites than

C. canadensis. *Calamagrostis stricta* favors mesic to hydric base-of-slope and valley bottom sites. *Calamagrostis nutkaensis* exhibits the widest range of conditions, from relatively dry ridge crests to valley bottom hydric moisture regimes, but is found only in the generally moist coastal climate.

The genus occurs over a wide range of substrate textures ranging from bedrock, to clay and peat. Two species, *C. purpurascens* and *C. sesquiflora*, favor bedrock or coarse textured substrates. Other species occasionally occur on these coarse substrates but are most abundant on medium to fine textures, especially silt to sand. *Calamagrostis stricta* and *C. montanensis* especially favor medium to fine textured soils. Generally the species grow over a wide range of soil chemistry, however, *C. canadensis* and *C. sesquiflora* are notably associated with acid sites, and *C. stricta* and *C. purpurascens* are associated with alkaline and limy soils.

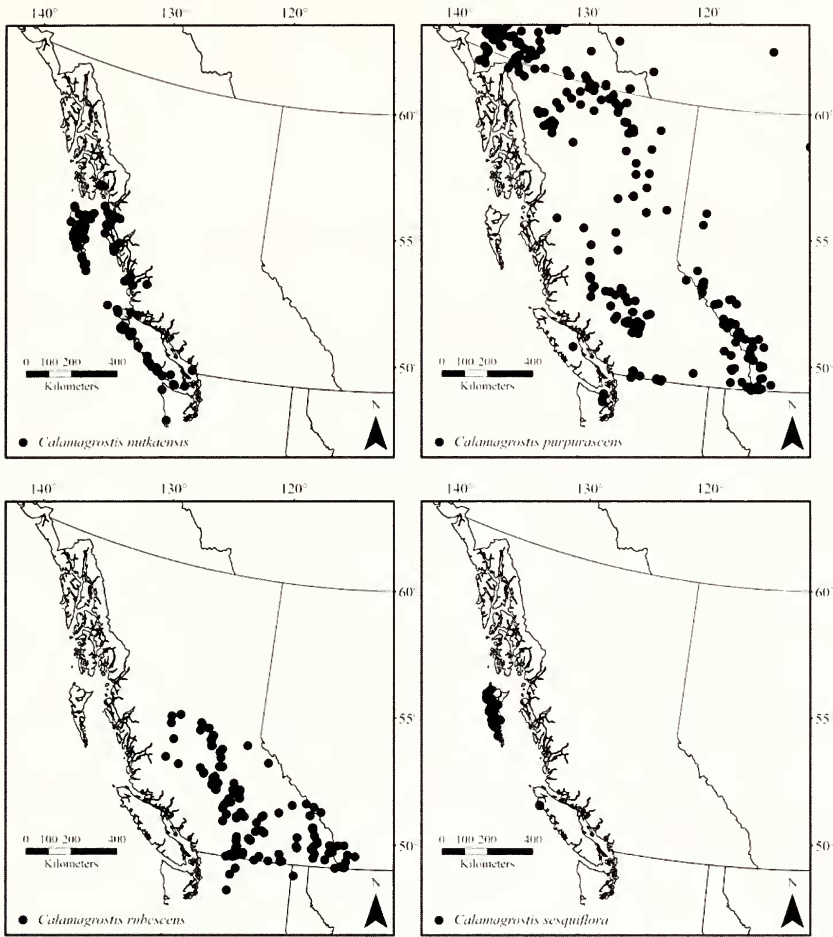


FIG. 2. Continued.

Species of *Calamagrostis* in western Canada, and in particular in British Columbia, have distinctive distributions (Fig. 2). Only two species, *C. stricta* and *C. canadensis*, occur throughout the

province and range widely in northwest North America (see figures in Marr et al. 2007). *Calamagrostis stricta* ranges from Alaska and Yukon southward into the western United States

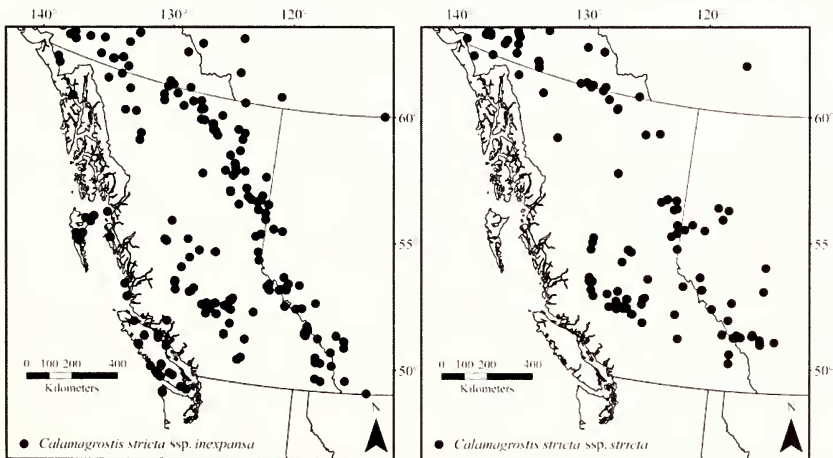


FIG. 2. Continued.

and eastward into Canada's prairie provinces and adjacent U.S. states. In British Columbia, to the extent that the two subspecies can be reliably distinguished, *C. stricta* subsp. *inexpansa* has the wider range, occurring both in the interior as well as on the coast including the Queen Charlotte Islands. *Calamagrostis stricta* subsp. *stricta* appears to be a strictly inland and relatively northern subspecies in British Columbia. The range dips southward in the Rocky Mountains, and it appears to be associated with cold continental climates. Globally *C. stricta* is a circumboreal/circumpolar taxon (Hultén 1968).

Calamagrostis canadensis occurs throughout the study area from Yukon across British Columbia southward into the Pacific Northwest states of the U.S. The range extends eastward into the Northwest Territories, Alberta and across Canada and the northeast U.S. (Marr et al. 2007). *Calamagrostis canadensis* var. *canadensis* is distributed throughout British Columbia except on the Queen Charlotte Islands and the extreme northwest. *Calamagrostis canadensis* var. *langsorfii* is recorded from all parts of the province, including the Queen Charlotte Islands and the northwest.

Two species, *C. sesquiflora* and *C. nutkaensis*, exhibit a strictly coastal distribution (Fig. 2): *C. nutkaensis* from California to coastal Siberia, *C. sesquiflora* from northern Vancouver Island to coastal northeast Asia (Hultén 1968; Hitchcock et al. 1969; Greene 1993). *Calamagrostis nutkaensis* occurs on or immediately adjacent to, the shoreline. Nearly all of the specimens from higher elevations were collected on the Brooks Peninsula (Ogilvie 1997) or on small islands near the mainland (e.g., Dundas Island). Plants from these locations are often shorter and have narrower leaves than those closer to sea level, however even at the higher elevations, there are specimens as tall as 1 m and with broad leaves. The distribution of *C. sesquiflora* is concentrated in the Queen Charlotte Islands, occurring elsewhere in BC only on the Brooks Peninsula, VI (Vancouver Island). This species was previously thought to occur as far south as Washington State, however plants from that area have recently been re-determined as *C. tacomensis* Marr and Hebda (Marr and Hebda 2006).

Three of the four remaining species (*C. lapponica*, *C. montanensis*, and *C. rubescens*) do not occur on the coast (Fig. 2). The fourth, *C. purpurascens* is widespread and occurs almost exclusively east of the Coast Mountain and Cascade-Coast Mountain crest well into the continent (Fig. 2). In 2008 this species was collected from mountainous inland Vancouver Island for the first time. There is also a notable near-coastal site for the species at high elevation on the relatively dry, east side of the Olympic Peninsula in Washington State.

The distribution of *C. rubescens* is strictly southern and inland within the study area with the northernmost occurrence near Francois Lake, British Columbia at 54.1°N latitude. The range remains largely inland until southern California where populations occur along the coast (Greene 1993).

Calamagrostis montanensis is largely a species of the continental plains, common in southern Alberta and adjacent U.S. states east of the continental divide. In British Columbia it is considered rare (Douglas et al. 2002a), occurring in the northernmost extension of the plains along the Peace River near Fort St. John and in the southern Rocky Mountain Trench where it has crossed the Rocky Mountain front.

In British Columbia, *C. lapponica*, a largely circumpolar species, occurs mostly north of 55.2°N. There are, however, isolated and disjunct populations in west central Alberta between 51.8 and 53.2°N on high mountain tops.

DISCUSSION

Taxa of Northwestern North American *Calamagrostis* and Their Distinguishing Features

Based on the multivariate analysis of morphological characters two groups of species emerge: 1) those that are relatively distinct; and 2) those in which there is some overlap in morphological characters and that are therefore more difficult to identify. In the relatively distinct group are *C. montanensis*, *C. purpurascens*, *C. rubescens*, *C. sesquiflora* and *C. nutkaensis*. Those that are more difficult to correctly identify belong to the *C. canadensis/C. lapponica/C. stricta* "complex". A comparison of Fig. 1C to Fig. 1D reveals that many specimens previously identified as *C. stricta*, *C. canadensis* or even *C. purpurascens* were re-determined in our analysis as *C. lapponica*, and vice versa. Further comparison of Figs. 1C and 1D indicates that the criteria that we used to distinguish between *C. canadensis* and *C. stricta* largely match the label determinations of the specimens at the species level, but less so at the infra-specific level. Although many specimens in this group are clearly distinct from each other, discrete clusters do not emerge in the scatter-plot of the PCA to the same extent as the other species. There are, however, morphological and ecological criteria by which these taxa can be distinguished and these are highlighted below.

Calamagrostis lapponica vs. *C. canadensis* and *C. stricta*. We distinguish *C. lapponica* from *C. stricta* and *C. canadensis* largely according to habitat and lower leaf surface texture (Table 2). Both *C. canadensis* and *C. stricta* are species of relatively moist even wet habitats (Crackles 1994; Cody 1996; Greene 2001), frequently occurring at

lower elevations than the largely alpine species *C. lapponica* (Table 3), although *C. canadensis* occasionally occurs in wet alpine meadows (and all of these are var. *langsdorfii*). On one occasion we collected *C. lapponica* growing in standing water, a very unusual habitat for this species. The lower leaf surface of *C. lapponica* is glabrous, whereas in *C. canadensis* and *C. stricta* it is scabrous. The number of nodes is particularly useful to distinguish *C. lapponica*, 1–2(3) nodes, from *C. canadensis*, (2)3–5(7) nodes, with which it is most frequently confused (compare Figs. 1C and 1D).

Using the preceding criteria, the specimens that we considered to best fit *C. lapponica* grouped together in the PCA analysis (Fig. 1C) and the habitat of these specimens generally matches descriptions from other parts of the species' range. In Europe, *C. lapponica* is largely an alpine species of "tundra, dry heaths and woods" (Clarke 1980). In Russia, *C. lapponica* occurs "In forest tundras, riverside sands and pebbles, sparse forests, among shrub; up to upper (bald) mountain peaks" Tsvelev (1984).

Calamagrostis canadensis vs. *Calamagrostis stricta*. Criteria to distinguish *C. canadensis* from *C. stricta* are difficult to circumscribe because many characters overlap (Table 2, Fig. 1C). Using Fig. 1C as a starting point, we designated specimens plotted to the left of "0" on the first axis as *C. stricta* (or *C. lapponica*) and those to the right of the "0" as *C. canadensis*. The characters for which there was little overlap between species and which accounted for most of the variation in the PCA included NODE, LIGHT, LIGL and BRL. *Calamagrostis canadensis* has (2)3–5(7) nodes, whereas *C. stricta* has 1–3(4) nodes. Ligules of *C. canadensis* are lacerate and fragile, whereas most *C. stricta* (and *C. lapponica*) specimens have relatively stiff ligules with entire margins. *Calamagrostis canadensis* ligules are generally longer ((1.5)3–8(12) mm) than those of *C. stricta* ((0.5)1–3.5(6) mm). There is little overlap in the length of the longest inflorescence branches (BRL), i.e., less than 37 mm in 92% of *C. stricta* specimens and greater than 37 mm in 75% of *C. canadensis* specimens.

Two ecological features also help to distinguish *C. canadensis* and *C. stricta*. In general, *C. stricta* appears to be associated with limy or alkaline substrates. In our experience, *C. stricta* is more likely to grow at the edge of, rather than in, wetland habitats as compared to *C. canadensis*. Where the two grow near each other *C. stricta* occurs "upslope" of *C. canadensis* and often at the edge or even just within forest, woodland or thicket.

Recognizing subspecific taxa. Our analyses uphold the recognition of subspecific taxa in *C. canadensis* and *C. stricta* but reveal that the entities are part of a morphological continuum, a

conclusion that matches that of Greene (1980). Most specimens of *C. stricta* in the lower part of Fig. 1C have glumes shorter than 3 mm long, whereas those that plot closer to *C. lapponica*, have glumes longer than 3 mm. This character primarily distinguishes subsp. *inexpansa* (glumes 3–4(4.8) mm) from subsp. *stricta* (glumes (2.2)2.5–3.0 mm). Using this criterion *C. stricta* subsp. *inexpansa* occurs on the coast as well as inland, whereas *C. stricta* subsp. *stricta* is an inland taxon only (Fig. 2). There also appear to be habitat differences between the two, with subsp. *inexpansa* growing in more forested habitats and subsp. *stricta* in more open habitats (Table 3). Hultén (1968) distinguished between these two taxa primarily by differences in callus hair length relative to the lemma, recognizing them at the specific rather than the subspecific level. He too mapped *C. neglecta* (Ehrh.) G. Gaertn. (*C. stricta* subsp. *stricta*) as primarily an inland species of coastal Alaska, and *C. inexpansa* (*C. stricta* subsp. *inexpansa* (A. Gray) C. W. Greene) along the coast as well as in the interior.

Glume characters also help distinguish varieties of *C. canadensis*. Nearly all specimens of *C. canadensis* that plotted below "0" on the second axis (Fig. 1C) have relatively glabrous glumes, shorter than 3.5 mm. These we designated as *C. canadensis* var. *canadensis* (glume length (2.5)3–3.5(4) mm). Those that occur above "0" have scabrous glumes longer than 3.5 mm, often with the scabrosity relatively long and sometimes bent. This second group we designated as *C. canadensis* var. *langsdorfii* (glume length (3.5)4–4.5(5.5) mm). All of the specimens labeled as *C. langsdorfii* from Russia are in this second group. The scabrosity of the glumes is mostly restricted to the keel in *C. canadensis* var. *canadensis*, whereas in *C. canadensis* var. *langsdorfii* they often cover the entire surface. Glume length to width differs as well, (2)2.5–3.5(4) for var. *canadensis* and (3)3.5–4(5.5) for var. *langsdorfii*, i.e., glumes of var. *langsdorfii* are more attenuate.

The characters by which *C. canadensis* var. *langsdorfii* is recognized here are consistent with Hitchcock et al.'s (1969:525) view. They questioned the occurrence of such an entity in North America, but concluded that if in fact it is the same as the Russian species, *C. langsdorfii*, that it should then be included in *C. canadensis* var. *scabra* (Kunth) Hitchc., which they distinguished primarily by the longer "rather strongly scabrous" glumes. However, as Greene (1980) indicates, *Calamagrostis scabra* J. Presl was published in 1830, whereas *C. langsdorfii*, was published in 1824. Our analysis (Fig. 1C) indicates that plants from Russia identified as "*C. langsdorfii*" are the same as *C. canadensis* var. *langsdorfii*.

The use of the aforementioned characters to define intraspecific taxa for *C. stricta* and *C.*

canadensis generates better defined clusters in the PCA, though there remains overlap (compare Figs. 1C, 1D). Despite the overlap, we believe that continuing to recognize subspecific taxa is appropriate, in part because the criteria that we used match subtle, but significant ecological differences (Table 3). Ecological differences are not so clear

in the case of *C. canadensis* subspecific taxa, nevertheless, there appears to be adequate morphological differentiation (glume size, shape and surface texture), to continue recognizing the two varieties. Whether or not these intraspecific taxa actually represent distinct lineages should be investigated using DNA markers.

KEY TO *CALAMAGROSTIS* OF BRITISH COLUMBIA

- 1a. Awns more than 4 mm long (total length); glumes distinctly keeled; awns bent, exserted; upper leaf blade glabrous, slightly scabrous, or densely tomentose; inflorescence less than 13 cm long; 1–3 nodes. 2
 2a. Upper blade surface tomentose; leaves flat or involute; awns 4–9 mm long; mostly east of the Coast Range. *C. purpurascens*
 2b. Upper blade surface glabrous to slightly scabrous; leaves flat; awns 5–13 mm long; Vancouver Island, Queen Charlotte Islands. *C. sesquiflora*
- 1b. Awns less than 4 mm long; glumes keeled or rounded; awns straight or bent, if exserted, then less than 2 mm beyond lemma margin; upper blade glabrous to scabrous, never densely tomentose; inflorescence usually longer than 5 cm; 1–7 nodes. 3
 3a. Callus hairs less than 60% of lemma length (observe here the callus, **not** the hairs of the rachilla) or the awn more than 1 mm longer than the lemma; glumes nearly glabrous; nodes 1–2(4). 4
 4a. Awns straight; plants strictly coastal, (within 10 km of coastline); collar not hairy; longest inflorescence branches 27–70 (105) mm long. *C. nutkaensis*
 4b. Awns bent; plants of the interior of the continent; collar often hairy; longest inflorescence branches (12)20–30(100) mm long. *C. rubescens*
- 3b. Callus hairs greater than 60% of the lemma length, if less than 60%, then the awn bent and less than 1 mm longer than the tip of the lemma or the glumes scabrous; nodes 1–5(7). 5
 5a. Awns always bent, lower blade surface scabrous; glumes and lemmas scabrous; leaves (1)2(3) mm wide; inflorescence less than (4)7–9(10) cm long, the longest branches less than 30 mm long; 1–2 nodes; dry prairies or grasslands, never alpine. *C. montanensis*
 5b. Awns nearly always straight; lower blade surface glabrous or scabrous; glumes and lemmas glabrous or scabrous; leaves 1–13 mm wide; inflorescence (4)8–15(25) cm long, the longest branches 14–120 mm long; 1–7 nodes; forest, wetlands or alpine. 6
 6a. Longest inflorescence branches more than 37 mm long, or if shorter, then the ligule tip delicate (i.e., easily torn) and lacerate; glumes scabrous on the keel and often throughout, the projections sometimes bent; leaves flat; the lower surface scabrous; (2)3–5(7) nodes. *C. canadensis*
 7a. Glumes usually less than 3.5 mm long; glumes acute, and scabrous on the keels, rarely throughout. var. *canadensis*
 7b. Glumes usually greater than 3.5 mm long, acuminate; glumes scabrous on the entire surface, the projections often bent. var. *langsдорffii*
- 6b. Longest inflorescence branches less than 37 mm long or if greater than 37 mm then the ligule stiff and entire; glumes glabrous to scabrous on the keels, but the projections never bent; leaves flat or involute, the lower surface glabrous or scabrous; 1–3(4) nodes. 8
 8a. Lower blade surface glabrous; leaves flat; glumes glabrous, rarely slightly scabrous on the keel, (3.5)4–5(5.5) mm long or more than 3 times longer than wide. *C. lapponica*
 8b. Lower blade surface glabrous or scabrous; leaves flat or involute; glumes glabrous to scabrous, (2.2)2.5–4(4.8) mm long, usually less than 3 times longer than wide. *C. stricta*
 9a. Glumes less than 3 mm long, glabrous to slightly scabrous and the callus hairs less than 2.5 mm long; culms usually smooth. subsp. *stricta*
 9b. Glumes more than 3 mm long, scabrous or the callus hairs more than 2.5 mm long; culms usually scabrous. subsp. *inexpansa*

Distributions of *Calamagrostis* Species in BC and Their Phylogeographical Significance

Extant *Calamagrostis* distributions can be understood in the context of Late Pleistocene history of habitats and glacial history. The most likely explanation for the strict coastal distribution of *C. nutkaensis* and *C. sesquiflora* is that they survived on the coast during late Wisconsin (Vashon) glaciations both south and north of the Cordilleran Ice sheet or in shoreline refugia (closed refugia *sensu* Lindroth 1969). The habitats for both likely existed along the immediate

shore zone even during the short interval of full-glacial conditions. *Calamagrostis nutkaensis* could have spread rapidly following deglaciation along the strandline and then moved a short distance inland into non-shoreline habitats such as bogs. *Calamagrostis sesquiflora* would seem to be well-adapted to persist on unglaciated headlands and ridges such as envisaged in coastal refugia (Calder and Taylor 1968; Hebda 1997; Ogilvie 1997). However, its apparent need for relatively mild winter temperatures and relative drought intolerance (as evidenced by its oceanic distribution) prevented spread inland on what

was a largely cold dry open landscape during glacial times (Hicock et al. 1982; Hebda and Whitlock 1997; Whitlock and Bartlein 1997; Heusser et al. 1999; Clague et al. 2004). The pattern of distribution of *C. sesquiflora* matches the disjunct ranges of other species with Vancouver Island/Queen Charlotte Island distributions such as *Ligusticum calderi* Mathias & Constance (Douglas et al. 2002a). Such distribution patterns are used as evidence of glacial refugia in these locations (Buckingham et al. 1995).

The mostly interior, middle- to high-elevation *C. purpurascens* likely survived throughout the unglaciated, inland landscape and then spread into previously glaciated BC from circum-glacial refugia where suitable habitats for it occurred (Hicock et al. 1982; Ritchie 1987; Thompson et al. 1993). It may also have survived in high elevation nunatak refugia. A hardy species of mesic to xeric ridge tops and upper slopes, it would have been well suited to cold windblown full-glacial sites before 14,000 years ago. Though ice sheets covered much of British Columbia and Alberta, refugia occupied by non-arboreal vegetation occurred, especially along the coast (Mathewes 1989; Hebda 1997; Brown and Hebda 2003; Fitton 2003) and possibly in northern B.C. (Marr et al. 2008).

Both of the continental inland species, *C. montanensis* and *C. rubescens*, likely spread north and west from the unglaciated zone south of the ice sheets as suitable, relatively warm habitats became available. Considering the once greater extent of warm and dry climates and open habitats of the early Holocene (Hebda 1995; Heinrichs et al. 2002), their ranges, especially that of *C. montanensis*, was likely greater than today having shrunk with the forest expansion of the past 7000 years. The spread of *C. rubescens* has likely been limited by conifer forest development, but during the middle and early Holocene, when forests were much more open it likely grew further north and at higher elevations than it does today.

The distribution and ecology of *C. lapponica* strongly suggest that it survived in the dry, cold, open landscape north of the Cordilleran and Laurentide ice-sheets during glacial times, and not south of these ice-sheets. Since the end of the ice age, it may have somewhat expanded its range southward, colonizing suitable high-elevation sites in the northern Rockies and further south into the Alberta Rockies. An alternative explanation for the Alberta sites would postulate that these populations are refugial relicts, remnants of a once more-continuous distribution. Extensive expansion after glaciation into southern alpine zones may not have been possible due to the rapid spread of conifers northward (MacDonald 1987). Our recent collections in northeast BC in the vicinity of Williston Lake and Tumbler Ridge

demonstrate that this species ranges further south in BC than was previously known.

The wide-ranging *C. canadensis* likely survived south and north of glacial ice sheets and then reinvaded glaciated terrain. *Calamagrostis canadensis* no doubt had abundant sites in which to thrive south of the Cordilleran-Laurentide ice system during the relatively moist Late Pleistocene time of extensive glacial lakes. This period of temporary separation may have contributed in part to the establishment or strengthening of differences between the two intraspecific taxa. Of the two subspecies, the hardier and widespread var. *langsdoerffii* may well have survived in and spread from Beringia. With warming and moistening climates, *C. canadensis*, especially var. *canadensis*, may have been dispersed rapidly to every suitable wetland site by birds (adhering to feathers), thus spreading rapidly across the entire region after deglaciation.

The wide-ranging distribution and similar, but not identical, habitats of *C. stricta* suggests a similar history to *C. canadensis*. However, the relatively-low upper-elevation distribution limit (Table 3) for *C. stricta* subsp. *stricta* suggests that it is less hardy than *C. canadensis* and may have come to occupy its North American range through northward migration from ice-free zones. The occurrence of *C. stricta* subsp. *inexpansa* as the only subspecific taxon on the coast is notable, because it suggests that the variety might be a pre-glacial entity isolated at one time from its vicariant partner, subsp. *stricta*. The distribution of subsp. *stricta*, coupled with the widespread occurrence until the Late Holocene of open habitats in the northwest interior of North America (Hebda 1995) strongly suggests a continental interior source of spread for this taxon.

CONCLUSIONS

Our study of *Calamagrostis* in British Columbia upholds the taxonomic entities recognized previously for the province, but provides a more satisfactory treatment and key for this difficult grass genus in a phytogeographically critical region of North America. Our results demonstrate that combining morphologic, ecologic and distribution data can be an effective way of clarifying the taxonomy of a group of morphologically similar taxa. We suggest that major collections need to re-examined and annotated so that regional distribution maps can be corrected. For example, some of the previously published (Greene 2001) maps of *Calamagrostis* species distributions in BC were in error based on mis-identifications; in particular, the following changes should be made: *C. lapponica* does not occur near Smithers, BC or at the BC-Washington border; *C. sesquiflora* does not occur near Prince Rupert, BC; in southern BC, *C. montanensis* does

not occur west of the Invermere area; *C. stricta* subsp. *stricta* does not occur in coastal BC.

Our study also points to several potential future investigations. A comprehensive DNA investigation would be particularly useful in elucidating the relationships of subspecific entities and species relationships in the *C. canadensis*, *C. stricta*, and *C. lapponica* complex, and could potentially test the new phylogeographical hypotheses that we have presented, if sufficiently variable DNA markers could be developed.

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APPENDIX I

SPECIMENS USED FOR MORPHOMETRIC ANALYSIS

Calamagrostis canadensis var. *canadensis*: CANADA. **Alberta:** Jasper National Park, Mt. Edith Cavell, 26 Aug 1917, *Macoun, J. M. 98153* (CAN); Rocky Mountain House, Foothills W of (M. D. Fairbarns study site), 5 July 1987, *Aiken, S. G. 44* (CAN). **British Columbia:** Big Bend, logbridge over Wood River where it enters the Columbia at, 100 mi N of Golden, 20 July 1941, *Weber, W. A. 2527* (CAN); Toad River, at mi 430 on route 96 between Mucho and Summit Lakes, 28 July 1968, *Morton, J. K. NA 1981* (CAN); Mount Robson Provincial Park, Moose Lake, Moose Lake marsh area, 27 Aug 1974, *Chuang, Ching Chang 1282* (V); Thompson-Okanagan, Cathedral Provincial Park, Lakeview Mountain, 19 Aug 1980, *Douglas, George W., Douglas, Gloria G. 12017* (V); Thompson-Okanagan, Cathedral Provincial Park, km 39 Ashnola Road, 11 June 1980, *Douglas, George W., Ratcliffe, Marilyn J., Douglas, G. A. 11771* (V); Liard River Repeater Valley, S aspect, Horseranch area, 21 Aug 1980, *Clement, Chris J. HR 8056* (V); Matthew River, flats on E side of, 17 Aug 1982, *Pavelick, Leon E. 82 348* (V); Kluskus, NW of Euchu Reach, plot BS-75-106, 27 Aug 1975, *Storey, Brenda BS-75-197* (V); Stikine River Kakuchuya Creek, S of, plot LM8025, 6 Aug 1980, *Clement, Chris J. LM 80143* (V); Peace River, Flatbed, mi 23.6 on Flatbed-Babcock Murray, plot number AH 76-066, 1976, *Harcombe, Andrew AH-139* (V); Cariboo-Chilcotin, Spokin Lake, 2 mi W of the lake, Moffat Creek Road junction, plot BS-76-035, 10 July 1976, *Storey, Brenda BS-76-66* (V); Peace River, Fort St. John, Watson Slough, 37 km SW of Fort St. John, 21 Jul 11, *Hebda, Richard J., Fitton, Richard 01-61* (V); Peace River, Fort St. John, Watson Slough, 37 km SW of Fort St. John, 21 July 11, *Hebda, Richard J., Fitton, Richard 01-64* (V); Peace River, W.A.C. Bennett Dam, 21 July 11, *Hebda, Richard J., Fitton, Richard 01-90* (V); Stikine District, Hackett River, at junction of Hackett and Shesley Rivers, 27 July 1971, *Schanen, Steven, Schanen, Sara 49,86* (V); Red Pass, 2 mi W of Red Pass Headquarters, 30 June 1974, *Chuang, Ching Chang 257* (V); Cheslatta Falls, 2 Aug 23, *Richard J. Hebda 00-09* (V); Cheslatta Falls, St. Mary's Lake, 2 Aug 23, *Richard J. Hebda 00-45* (V); **Yukon:** Liard River, NW of Watson Lake, 10 Aug 1980, *Oswald, E. T. YT-13* (V); Dezadeash River Valley, St. Elias Mountains, 30 July 1967, *Pearson, A. M. 67-313* (CAN); Mayo, 2 Aug 1949, *Gillett, J. M., Calder, J. A. 4246* (DAO); Coal River Springs, Coal River Springs proposed park, Site 5, E of Site 4., 6 July 1983, *Kennedy, Catherine 34* (DAO); Twin Lakes Campground, Klondike Hwy, km 310, 20 July 1980, *Cody, W. J. 28188* (DAO).

Calamagrostis canadensis var. *langsдорffii*: CANADA. **British Columbia:** Cluculz Lake, E of Vanderhoof, 29 June 1944, *Eastham, J. W. 11726* (CAN); Summit Pass, vicinity of Pass, Rocky Mountains, 25 July 1948, *Raup,*

- Hugh M., Correll, D. S. 10826* (CAN); Ootsa Lake, Alcan Campground, 2 Aug 24, *Richard J. Hebda 00-81* (V); Prince Rupert Forest Region, Telkwa Range, headwaters of Glacis Cr., 2 Sep 1989, *Pojar, J. JP890038* (SMI); Nulki Lake, SW of Vanderhoof, 14 Aug 1945, *Munro, J. A. s.n.* (V); Van Horlick Creek, near head of E branch, S of Duffy Lake, 4 Sep 1976, *Pojar, James J. 760543* (V); Vancouver Island, Enos Lake, along W shore of lake, 8 June 1981, *Power, R., Waterhouse, M. 22* (V); Vancouver Island, Haley Lake, Vancouver Island (V); Tatisno Mountain, N of Kitza Lake, 19 Aug 1979, *Ceska, Adolf, Ceska, Oldriska, Polster, David F., Martens, Brian 3774* (V); Nadina Lake, Hummock N of Nadina Lake Road, Plot TH-80-04, 12 Aug 1980, *Thompson, C. CT80-36* (V); Timothy Mountain, 14 July 1981, *Thompson, C. CT81-112* (V); Cariboo, Big Loon Lake, 1 mi from the W tip of the lake, 12 July 1976, *Storey, Brenda BS-76-101* (V); Far Creek, plot DR#8a, 24 July 1979, *Harcombe, Andrew AH-79-118* (V); Peace River, Stewart Creek, area on Codner Coldstream, 15 Aug 1979, *Ferster, Rick RF-79-298* (V); Thompson-Okanagan, Hardie Hill, Dewdrop, 21 Sep 1981, *Lea, T. T-81-130* (V); Richardson Lake, E.P. 1046, approx. 55 km SW of Burns Lake, Aug 1989, *Trowbridge, R., Thomson, S. s.n.* (V); Thompson-Okanagan, Ridge Lake, near Kamloops, 31 July 1963, *Pringle, William L. s.n.* (V); Salahagen Creek, Upper Kimsquit near Salahagen Creek, 23 July 1983, *Clement, Chris J. 83132* (V); Flannigan Slough, Taku River area, S end of Flannigan Slough, 10 July 1982, *Ceska, Adolf, Ceska, Oldriska, Parisien, L. 12069* (V); Peace River, Watson Slough, 37 km SW of Fort St. John, 21 July 11, *Hebda, Richard J., Fitton, Richard 01-63* (V); Gwillum Lake Road, 10 July 1976, *C. Clement CJC-70* (V); Haines Road, km 147, near edge of small lake, 19 July 1979, *Douglas, George W., Ratcliffe, Marilyn J. 11356* (V); Puggins, Mount, lower end of Puggins Mt. road, 9 July 1979, *Pavlick, Leon E., Taylor, B. 79-515* (V); Cumberland Creek, Skeet Club, swamp (V). **Yukon:** Sheldon Lake, 2 July 19, *Cody, W. J., Cody, D. W. 36954* (DAO); Pintail Slough, Old Crow Flats, 12 Aug 1976, *Russell, Don 26* (V); Mt. White, Valley slopes and mountain summits about 7 mi E of Little Atlin Lake, 19 Aug 1943, *Raup, Hugh M., Correll, D. S. 11434* (CAN); Red Tail Lake, mountain slopes and summits NE of Red Tail Lake, 9 July 1948, *Raup, Hugh M., Drury, W. H., Raup, K. A. 13480* (CAN); Canol Rd., km 312, 29 July 1981, *Hodgson, Vaughn 433* (DAO); Contact Creek Ezzo Station, Alaska Hwy, km 949.5, 9 July 1983, *Cody, W. J. 32507* (DAO); Tom Creek, area, 13 July 1980, *Rosie, R. 951* (V); Tom Creek., 15 July 1980, *Rosie, R. 1410* (V); Kluane National Park, Onion Lake, ca. 46 mi S of Haines Junction, 12 Aug 1973, *Douglas, George W., Douglas, Gloria G. 7084* (V); Dry Creek, S of the creek, Mile 1184 Alaska Highway, 27 July 1977, *Douglas, Gloria G., Tait, V. L. 10459* (V). **RUSSIA:** 133827, (V); 133872, 5 Aug 1978, (V); 133861, 24 July 1964, (V); 143959, 26 Aug 1986, (V).
- Calamagrostis lapponica*.** CANADA. **Alberta:** Clearwater Forest Reserve, Baldy Mountain, summit and upper slopes of, N of Nordegg., 18 Aug 1957, *Porsild, A. E. 20599*, (CAN); Cadomin, S.W.26-45-23-W.S.M., 20 Aug 1967, *Pegg, George 2685*, (DAO). **British Columbia:** Birch Mountain, N slope of, Teresa Island, Atlin Lake, 12 Aug 1975, *Buttrick, Steven 747*, (DAO); Cassiar, Looncry Lake, 2 Sep 1964, *Ritcey, Ralph 14*, (V); Cassiar, Dall Lake, 13 July 1961, *Ahti, Leena, Ahti, Teuvo 6909*, (V); Silvertip Mountain, Tootsee Valley, 13 Aug 1995, *Doucet, R., Beaulieu, G. 161*, (V); Liard River Basin Petitot River, edge of outline in moist forest site, 31 July 1974, *Haber, Eric, Bergeron, J. 2285*, (V); Gladys Lake Ecological Reserve, Ptarmigan Ridge, SE face, 16 July 1975, *Pojar, James J. 111d*, (V); Stikine District, Gladys Lake Ecological Reserve, Landslide Ridge, Ghost Mountain, 8 July 1975, *Pojar, James J. 76e*, (V); Gladys Lake Ecological Reserve, Maternity Mountain, 25 July 1975, *Pojar, James J. 144g*, (V); Stikine River Spatsizi Plateau, above headwaters of Black Fox Creek, 8 Aug 1975, *Pojar, James J. 198*, (V); Swift River, 10 km SW of, 28 July 1980, *Brayshaw, T. Christopher 80-160*, (V); Horseranch, N end of Horseranch, 24 Aug 1980, *Clement, Chris J. HR 8094*, (V); Horseranch Lake, N end of, 24 Aug 1980, *Clement, Chris J. HR8095*, (V); Garbutt Creek, Garbutt Creek area, 25 Aug 1979, *Ceska, Adolf, Ceska, Oldriska, Polster, David F., Martens, Brian 3562*, (V). **Northwest Territories:** MacKenzie district, Eskimo Lake Basin, outlet of Sitidgi Lake, 11 Aug 1957, *Cody, W. J., Ferguson, D. H. 10815*, (SMI). **Yukon:** Ptarmigan Heart, mountain slopes and summits NE of Ptarmigan Heart, 13 July 1948, *Raup, Hugh M., Drury, W. H., Raup, K. A. 13618*, (CAN); Tatshenshini River, mi 100, Haines Highway, 14 Aug 1957, *Schofield, W. B., Crum, H. A. 8265*, (CAN); Little Atlin Lake, Valley slopes and mountain summits, 13 Aug 1943, *Raup, Hugh M., Correll, D. S. 11287*, (CAN); Ptarmigan Heart, mountain slopes and summits NE of Ptarmigan Heart, 16 July 1948, *Raup, Hugh M., Drury, W. H., Raup, K. A. 13720*, (CAN); LaBiche River area, Kotaneelee Range, 20 June 1998, *Rosie, Rhonda 2069*, (DAO); Otter Lake, above lake S of Itsei Range, 2 Aug 1960, *Calder, J. A., Kukkonen, I. 27759*, (DAO); Kusawa Lake, mountain between Kusawa Lake and Jojo Lake, 19 Sep 1997, *Bennett, B. 97-672*, (DAO); Deep Creek, about 2 mi from the Arctic Ocean, 16 Aug 1976, *Russell, Don 4*, (V); Ferry Hill, 9 Aug 1977, *Rosie, Rhonda 474*, (V); Mt. Laborite, 20 July 1994, *Zoladeski, Chris 200*, (DAO). **USA. Alaska:** Nabesna Rd, mi 89, 24 July 1947, *Dutilly, LePage and O'Neill 21563*, (DAO); Kurupa Valley, western side of Kurupa Valley about 8 mi NW of Kurupa Lake, 3 Aug 1952, *Riedeman, Robert s.n.*, (DAO); King Salmon, 8 Aug 1952, *Schofield, W. B. 2653*, (DAO); Eastern Brooks Range, Porcupine Lake, 24 July 1979, *Gustafson, Karen s.n.* (V).
- Calamagrostis montanensis*.** CANADA. **Alberta:** Livingston Valley, at the gap, 11 Aug 1915, *Malte, M. O 108222* (DAO); Cowley, SE of, 9 Aug 1939, *Moss, E. H. 345* (DAO); Carway, at U.S. border, 15 mi S of Cardston, 2 Aug 1950, *Dore, W. G. 12269* (DAO); Wapato River, Wembley Region, S of Wembley, 8 July 1976, *Barkworth, M. 1459* (DAO); Tough Creek, extreme SW corner, sect 17, S of, 28 July 1982, *Aiken, S. G., Darbyshire, S. J., Khumph, Bud 2506* (DAO). **British Columbia:** Invermere, Old Fort Community Hall, Columbia Valley, 16 July 1947, *Eastham, J. W. 15930* (DAO); Windermere Beach, 28 July 1947, *Eastham, J. W. 15920* (DAO); Invermere, Old Fort Community Hall, Columbia Valley, 16 July 1947, *Eastham, J. W. 15930* (DAO); Kootenay, Invermere, 11 Aug 1943, *Eastham, John W. 11106* (V); Kootenay, Edgewater, between Sinclair Creek and Edgewater, Columbia Valley, 29 July 1947, *Eastham, John W. s.n.* (V); Kootenay, Invermere, Old Fort Community Hall, 16 July 1947, *Eastham, John W. s.n.* (V); Kootenay, Windermere Lake, Columbia Valley, above Wind-

ermere Beach, 28 July 1947, *Eastham, John W.* 20.949 (V); Kootenay, Fairmont Hot Springs, one mi N of, 2 July 1948, *Eastham, John W.* s.n. (V); Peace River, Clayhurst Ecological Reserve, Doe Creek, 29 July 1969, *Brayshaw, T. Christopher* 5352 (V); Kootenay, Invermere, 1 July 1947, *Fodor, Fred* s.n. (V); Kootenay, Wilner Marsh, slope above, Plot 6102-01, 13 June 1981, *Lea, T.* TL-81-06 (V); Kootenay, Radium, N-most highway viewpoint S of Radium, 1.7 km S of main intersection of Radium, 25 Aug 1995, *Roemer, Hans L.* 95077 (V); Alces River, 26 July 1995, *Douglas, George W.*, *Djan-Chekar, Nathalie* 13060 (V).

***Calamagrostis nutkaensis*. CANADA. British Columbia:** Mayer Lake, S end of lake, W of Tlell, Graham Island, 20 Aug 1964, *Calder, J. A.*, *Taylor, R. L.* 36105 (DAO); Prince Rupert, 30 July 1916, *Malte, M. O.* 106868 (DAO); Inslung Bay, near Bay, Langara Island off NW tip of Graham Island, 16 July 1957, *Calder, J. A.*, *Savile, D. B. O.*, *Taylor, R. L.* 22534 (DAO); Vancouver Island, Kyuquot, Markale, 3 Aug 1957, *Bell, Marcus, Davidson, John* 767 (V); Queen Charlotte Islands, Tow Hill, Graham Island, 30 May 1963, *Young, A.*, *Hubbard, W.* 110 (V); North Coast, Digby Island, Prince Rupert Airport, 9 Aug 1973, *Brayshaw, T. Christopher* s.n. (V); Vancouver Island, Cape Scott, near lighthouse, 22 July 1982, *Pavlick, Leon E.* 82-60 (V); Queen Charlotte Islands, Rennell Sound, Re9B4, 27 July 1982, *Ryan, Michael W.* 2 (V); Brooks Peninsula, Cladothamnus Lake, Ridge Quadrant, Ridge SW above lake, 9 Aug 1981, *Ogilvie, Robert T.*, *Hebda, Richard J.*, *Roemer, Hans L.* 81893 (V); Gillen Harbour, head of Harbour, Dewdney Island, 13 July 1984, *Ogilvie, Robert T.*, *Roemer, Hans L.* 8471318 (V); Dewdney Island, SW peninsula of, 13 July 1984, *Ogilvie, Robert T.*, *Roemer, Hans L.* 8471354 (V); Dewdney Island, head of Gillen Harbour, 13 July 1984, *Ogilvie, Robert T.*, *Roemer, Hans L.* 8471319 (V); Brooks Peninsula 1900 Peak, Lagoon Quadrant, 1900 Peak, 9 Aug 1984, *Ogilvie, Robert T.*, *Schofield, Wilfred J.*, *Hebda, Richard J.* 848932 (V); Vancouver Island, Pacific Rim National Park, Nettle Island, near camp, Barkley Sound, Broken Islands, 8 Aug 1982, *Ogilvie, Robert T.*, *Hebda, Richard J.* 828089 (V); Central Coast, Dundas Islands, Zayas Island, 25 July 1987, *Ceska, Adolf, Ceska, Oldriska, Ogilvie, Robert T.* 22032 (V); Vancouver Island, Bamfield, SW of Bamfield, 22 Aug 1980, *Ogilvie, Robert T.* s.n. (V); Queen Charlotte Islands, Geikie Creek, Graham Island, 200 m S of Geikie creek #3, 50 m E of highway 16, 22 Aug 1997, *Lomer, Frank, Grove, N.* 97529 (V); Gulf Islands, Egeria Mountain, Southern Bowl, Porcher Island, 8 Aug 1987, *Ceska, Adolf, Ceska, Oldriska* 22649 (V); Central Coast, Dundas Islands, Zayas Island, 25 July 1987, *Ceska, Adolf, Ceska, Oldriska, Ogilvie, Robert T.* 22053 (V); Central Coast, Campbell Island, N of Bella Bella (Waglisla), Wag air fueling station, 19 July 1999, *Hebda, Richard J.* s.n. (V).

***Calamagrostis purpurascens*. CANADA. Alberta:** Jasper National Park, Mt. Edith Cavell, 28 Aug 1964, *Calder, J. A.* 37200 (DAO); Jasper National Park, Lake Edith, YMCA Lodge, 4 July 1955, *Jenkins, L.* 5817 (DAO). **British Columbia:** Cariboo, Mt. Begbie, 23 June 1944, *Eastham, John W.* 17026 (V); Cariboo-Chilcotin, Sinkut Mountain, near Vanderhoof, 18 July 1945, *Eastham, John W.* 18828 (V); Cassiar District, Cassiar, 18 June 1956, *Taylor, Thomas M. C.*, *Szczawinski, Adam F.*, *Bell, Marcus* 391 (V); Cariboo, Mt. Pope, a few mi NW of Fort St. James, 11 July 1892, *Hatcher, J.* s.n.

(V); Liard River, Liard Hot Springs Park, 16 Aug 1971, *Brayshaw, T. Christopher, Barrett, David* s.n. (V); Liard River, Liard Hot Springs Provincial Park, Mt. Ole, 7 July 1971, *Brayshaw, T. Christopher, Barrett, David* s.n. (V); Cariboo-Chilcotin, Taseko River, valley side on E by Taseko River Rd, 14 July 1978, *Pavlick, Leon E.*, *Sax, Michael* 78-571 (V); Hutchison Lake, near lakes, 21 Aug 1979, *Ceska, Adolf, Ceska, Oldriska, Polster, David F.*, *Martens, Brian* 8061 (V); Buckley Creek, above Klastline River, upstream Buckley Creek, 29 Aug 1979, *Ceska, Adolf, Ceska, Oldriska, Polster, David F.* 8073 (V); Kootenay, Flathead, two ridge tops in S, ca. 5 mi from Canada-US border, July 1973, *Dick, John* FR24 (V); Kootenay, Skookumchuck, 0.1 mi up Regional Garbage Dump Rd, 2 July 1976, *Ferster, Rick* 76-78 (V); Dean River, Upper Dean River Rd, plot number 2803-79, 1979, *Harcombe, Andrew* AH-79-30 (V); Stikine River, Telegraph Creek, slopes above Day's Ranch, 10 June 1980, *Ceska, Adolf, Ceska, Oldriska, Polster, David F.* 4070 (V); Cariboo-Chilcotin, Cheslatta, Kritchlow property, 1 km E of Cheslatta, 21 July 12, *Hebda, Richard J., Fitton, Richard* 01-119 (V); Tanzilla River above the river, 2 km above junction with Stikine River, 10 July 1980, *Ceska, Adolf, Ceska, Oldriska, Polster, David F.* 8054 (V). **USA. Alaska:** Talkeetna Mts., 2 Sep 1978, *Talbot, S. S.* T8023-V-15 (DAO). **Washington:** Buckhorn Mt., T27N R4W S13 SE1/4, 8 June 1979, *Buckingham, Nelsa* 2129 (OLYM); Olympic National Park, Royal Basin, RB2, Ridge between Royal Creek and Dungeness River, Aug 1983, *Dalton, Burger* 2656 (OLYM).

***Calamagrostis rubescens*. CANADA. British Columbia:** Bear Cr. Falls, N of Clearwater station, Bear Cr. Falls, 10 Aug 1956, *Calder, J. A.*, *Parmelee, J. A.*, *Taylor, R. L.* 19916 (DAO); Invermere, 31 July 1915, *Malte, M. O.* 108288 (DAO); Quesnell, S. of Quesnell, 14 July 1982, *Aiken, S. G.*, *Darbyshire, S. J.*, *Roberts, A.* 2320 (DAO); Alexis Creek, 16 July 1982, *Aiken, S. G.*, *Darbyshire, S. J.* 2365 (DAO); Saxton Lake, 21 July 2008, *Richard J. Hebda, Richard Fitton* 00-37 (V); Cariboo-Chilcotin, Vanderhoof, 15 Aug 1919, *Macoun, John M.* 27 (V); Kootenay, Cranbrook, 7 Aug 1943, *Eastham, John W.* 16385 (V); Cariboo-Chilcotin, Riske Creek, N slope, SW of Beecher Dam, 3 Oct 1968, *Brayshaw, T. Christopher* s.n. (V); Thompson-Okanagan, Manning Provincial Park, Wrangler Station, approximately one half mi from Nature House, 16 Aug 1973, *Chuang, Ching Chang* 1259 (V); Lower Fraser Valley, Ross Lake, 1 mi N of International Boundary on Ross Lake Rd, 20 July 1971, *Smith, R. B.* 29 (V); Kootenay, Arrow Lakes, area, 12 June 1975, *Polster, David* s.n. (V); Kootenay, Akamina Creek, 0.8 km downstream from Gloyne Camp on N side of road, 21 Aug 1975, *Polster, Alan, Plug, Egbert, Polster, David* 80:14 (V); Cariboo-Chilcotin, Riske Creek, south creek area, 11 July 1978, *Pavlick, Leon E.*, *Sax, Michael* 78-452 (V); Cariboo-Chilcotin, Dragonfly Lake, E of Dragonfly Lake, near Deka Lake, 13 July 1972, *Resource Analysis Branch, Kelowna* 72-92 (V); Kootenay, Argenta, Johnson's Landing, 6 mi S of Argenta-Johnson's Landing intersection, 15 June 1982, *Wood, Terry* 822085 (V); Kootenay, Harmer Ridge, Natal, 30 July 1973, *Dick, John* HR 9 (V); Thompson-Okanagan, Peachland Creek, Peachland Creek area, 8 July 1987, *Pavlick, Leon E.* 87-282 (V); Cariboo-Chilcotin, Dragonfly Lake, E of Dragonfly Lake, near Deka Lake, 13 July 1972, *van Barneveld, Jim W.* JvB-72-92 (V); Cariboo-Chilcotin,

Oregon Jack Creek, 5 July 1978, *Pavlick, Leon E., Sax, Michael* 78-271 (V).

***Calamagrostis sesquiflora*. CANADA. British Columbia:** Queen Charlotte Islands, Bigsby Inlet, head of Bigsby Inlet, opposite Lyell Island, E coast of Moresby Isl., 5 July 1957, *Calder, J. A., Taylor, R. L., Saville, D. B. O.* 22141 (DAO); Queen Charlotte Islands, Mt. de la Touche, Farifax Inlet, Tasu Sound, west coast of Moresby Isl., 16 Aug 1957, *Calder, J. A., Taylor, R. L.* 23571 (DAO); Queen Charlotte Islands, Mosquito Lake, Mt. above Mosquito Lake near head of Cumshewa Inlet, 24 Aug 1957, *Calder, J. A., Taylor, R. L.* 23753 (DAO); Queen Charlotte Islands, Victoria Lk., Upper Victoria Lk., near S end Moresby Isl, 5 July 1964, *Calder, J. A., Taylor, R. L.* 35718 (DAO); Queen Charlotte Islands, Cumshewa Inlet, 3 mi W of head of Cumshewa Inlet below N face of Mt. Moresby, 1 Aug 1964, *Calder, J. A., Taylor, R. L.* 36507 (DAO); Queen Charlotte Islands, Graham Island, E side of Shields Bay, Rennel Sound, W coast of the island, 16 July 1963, *Brassard, Hainault* 2824 (V); Brooks Peninsula, Ridge Quadrant, Ridge SW above Cladthamnus Lake, 9 Aug 1981, *R. T. Ogilvie, R. J. Hebda & Hans L. Roemer* 81894 (V); Vancouver Island, Brooks Peninsula, Cassiope Pond, ridge quadrant, crest of ridge E of the pond, 31 July 1981, *Ogilvie, Robert T., Hebda, Richard J., Roemer, Hans L.* 8173113 (V); Vancouver Island, Doom Mt., summit of main peak, ridge quadrant, Brooks Peninsula, 17 Aug 1981, *Ogilvie, Robert T., Hebda, Richard J., Roemer, Hans L.* 8181711 (V); Vancouver Island, Brooks Peninsula, July 1978, *Roemer, Hans L.* 7890 (V); Queen Charlotte Islands, Chanal, Port, W Graham Island, July 1979, *Roemer, Hans L.* 79159 (V); Queen Charlotte Islands, Takakia Lake, North Ridge, 19 July 1980, *Ogilvie, Robert T., Roemer, Hans L., Mersereau, W. O.* s.n. (V); Anna Lake, North end, upper waterfall, 25 Aug 1992, *Ogilvie, Robert T. s.n.* (V); Queen Charlotte Islands, Mount Laysen, 20 Aug 1992, *Ogilvie, Robert T. s.n.* (V); Queen Charlotte Islands, Dinan Creek, on mountain ridge, at headwaters of Dinan creek, Graham Island, 17 July 1997, *Lomer, Frank, Grove, N.* 97386 (V); Queen Charlotte Islands, Apex Mt., 3 km W of Apex Mt., Moresby Island, 19 Aug 1997, *Lomer, Frank, Grove, N.* 97448 (V); Queen Charlotte Islands, Moresby Island, Mosquito Mt., 25 km SSW from Queen Charlotte City, 20 Aug 1997, *Lomer, Frank, Grove, N.* 97498 (V).

***Calamagrostis stricta* subsp. *inexpansa*. CANADA. Alberta:** Beaverlodge, 17 July 1921, *Malte, M. O.* 106930 (DAO); Willow Creek, Willow Cr. area, Jasper NP, 1978, *Reynolds, H.* J75 (DAO). **British Columbia:** Noralee, Francois Lake, above Brewer's, 8 July 1944, *Eastham, J. W.* 11866 (CAN); Buckingham River, 31 Aug 1943, *Raup, Hugh M., Correll, D. S.* 11592 (CAN); Queen Charlotte Islands, Delkatla Inlet, just E of Masset, Graham Island, 3 Oct 1968, *Brayshaw, T. Christopher s.n.* (V); Peace River, Portage Mt., Portage Mt. Dam, small lake beside the BC Hydro camp, 25 July 1965, *Szczawinski, Adam F.* 8165 (V); Alsek River, Tatshenshini River, junction of, 24 June 1975, *Brayshaw, T. Christopher, Carriagan, C. J. s.n.* (V); Kootenay, Mt. Robson Provincial Park, S of Nature House along Fraser River, 22 July 1975, *Chuang, Ching Chang* 75175 (V); Vancouver Island, McCreight Lake, 7 Oct 1977, *Brayshaw, T. Christopher s.n.* (V); Pacific Rim National Park, Klanawa River, 11 July 1973, *Hartwell, Sharon* 71105 (V); Vancouver Island, Wickaninnish Bay, along Long Beach near the mouth of Sandhill

Creek, 20 June 1969, *Soper, James H., Brayshaw, T. Christopher, Shchepanek, Michael J.* 12307 (V); Beaverdam Lake, 18 Aug 1978, *Brayshaw, T. Christopher* 78-677 (V); Stikine District, Kuachon Lake, NE of Kuachon Lake Lodge, 29 Aug 1979, *Ceska, Adolf, Ceska, Oldriska, Polster, David F.* 4163 (V); Narraway River, E of Manitou Mtn., 18 Aug 1977, *Ceska, Adolf, Wood, Terry* 9289 (V); Kootenay, Tete Jaune Cache, on Highway 5 near, 8 July 1977, *Ceska, Adolf, Wood, Terry* 9290 (V); Vancouver Island, Farewell Lake, N of Campbell River, 16 Aug 1983, *Ceska, Adolf, Ceska, Oldriska* 16283 (V); Vancouver Island, Pacific Rim National Park, Effingham Island, Barkley Sound, Broken Islands Group, 8 Aug 1982, *Ogilvie, Robert T., Hebda, Richard J.* 828083 (V); Thompson-Okanagan, Minnie Lake, by pothole lake just N of, 5 July 1987, *Pavlick, Leon E.* 87-168 (V); Kootenay, Ewin Creek, 0.8 mi SW of Ewin Creek on Main Fording Coal Rd, 9 Sept 1977, *Ferster, Rick* 77-98 (V); Vancouver Island, Keeha Beach, delta of Keeha Creek, 23 June 1983, *Ogilvie, Robert T. s.n.* (V); Gulf Islands, Trial Island, 20 July 1976, *Ceska, Adolf, Ceska, Oldriska s.n.* (V); Atlin, around Tarahne steamboat and Atlin Inn, 15 July 1982, *Ceska, Adolf, Ceska, Oldriska, Goward, Trevor* 12649 (V); One Fifteen Creek, mi 406, 3 km W of 115 Creek picnic site, 26 July 1982, *Ceska, Adolf, Ceska, Oldriska, Goward, Trevor* 13469 (V); Vern Ritchie Glacier, foreland of glacier, Haines Triangle, 26 July 1992, *Pojar, James J.* JP920156 (V); Peace River, Cecil Lake, off Road #245, enclosures near lake, 25 June 1997, *Ceska, Adolf* 30730 (V). **Yukon:** Canol Rd., lower part of Canol road, along the road, 13 July 1947, *Porsild, M. P., Porsild, R. T.* 506 (CAN); Hunker P.O., 8 July 1950, *Campbell, John D.* 50 (DAO); Eagle Plains, E of the Richardson Mtns., July 1979, *James, T. D. W.* 17 (DAO); Haines Junction, on Haines Highway S of Haines Junction, 26 July 1980, *Cody, W. J., Ginns, J. H.* 28384 (DAO); Hyland River, 25 July 1994, *Brunner, Greg* 84 (DAO); Itsi Range, unnamed lake in range near Yukon-McKenzie border, 31 July 1960, *Calder, J. A., Kukkonen, I.* 27642 (DAO); Klondike Highway, km 656, 19 July 1980, *Cody, W. J.* 28090 (DAO); Canol Rd, 10 km, 1 Aug 1980, *Cody, W. J., Ginns, J. H.* 28767 (DAO); Dawson, along bank of Yukon River at Dawson., 18 July 1930, *W. J. G. s.n.* (V).

***Calamagrostis stricta* subsp. *stricta*. CANADA. Alberta:** Pigeon Lk., 15 Aug 1945, *Turner, G. H.* 4680 (DAO); Pigeon Lake, Opposite Ma-Me-O Beach on Pigeon Lk., 29 July 1947, *Turner, G. H.* 5927 (DAO); Falher, 19 July 1948, *Jenkins, L.* 566 (DAO); Manyberries, 17 June 1937, *Campbell, J. A. s.n.* (DAO). **British Columbia:** Kleena Kleene, 3.5 mi W of Kleena Kleene P.O., 5 July 1956, *Calder, J. A., Parmelee, J. A. Taylor, R. L.* 19196 (DAO); Cariboo-Chilcotin, Burns Lake, swamp at Tatlarose S of lake, 9 July 1944, *Eastham, John W.* 17759 (V); Stikine District, Lake Tatogga, NE end of, 10 Aug 1971, *Brayshaw, T. Christopher, Barrett, David s.n.* (V); Barney Lake, mi 581, Alaska Hwy, 1 Aug 1974, *Brayshaw, T. Christopher, Polster, David F. s.n.* (V); Peace River, Stony Lake, 17 mi N of, Peace River, district, 5 Aug 1976, *Chuang, Ching Chang* 493 (V); Fletcher Lake, 3.2 km NE of, 5 Aug 1978, *Thompson, Carol E. s.n.* (V); Peace River, Bear Flat, Bear Flat area, 19 July 1979, *Pavlick, Leon E., Taylor, B.* -797 (V); Cariboo-Chilcotin, Hooch Lake, S of, ca. 15 km SW of Nimpo Lake, 7 July 1980, *Annas, Richard, Ruyle, Gloria G., Nicholson, Allison,*

Coupe, Ray 80-272 (V); Liard River Basin, Coal River, N of, 20 Aug 1979, *Ceska, Adolf, Ceska, Oldriska, Polster, David F., Martens, Brian 3726a (V)*; Upper Dean River, plot number PR#4, 16 July 1979, *Harcombe, Andrew AH-79-40 (V)*; Cariboo-Chilcotin, Lessard Lake, N of the lake, plot no. Dr#7, 22 July 1979, *Harcombe, Andrew AH-79-101 (V)*; Peace River,

Watson Slough, 37 km SW of Fort St. John, 21 July 11, *Hebda, Richard J., Fitton, Richard 01-56 (V)*; Cheslatta Lake, floodplain, 2 Aug 23, *Richard J. Hebda 00-21 (V)*. **Yukon:** Kluane National Park, Haines Junction, one mi N of the junction of Kawkawulsh and Dezadeash Rivers and ca. 10 mi WSW of Haines Junction, 1 Aug 1973, *Douglas, G. W., Douglas, G. G. 6682 (CAN)*.